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Oak decline and red oak borer outbreak: impact in upland oak-hickory forests of Arkansas, USA

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Summary

Oak-hickory forests in the Ozark and Ouachita Mountains of Arkansas recently experienced an episode of oak mortality in concert with an outbreak of the red oak borer (*Enaphalodes rufulus* (Haldeman) (Coleoptera: Cerambycidae)). We utilized data from the Forest Inventory and Analysis (FIA) program of the USDA Forest Service to explore changes in percent red oak (*Quercus* subgenus *Erythrobalanus*) mortality as a function of standing trees, basal area and stem density during and after the recent borer outbreak throughout the state of Arkansas. Mean red oak mortality levels in Arkansas FIA oak-hickory plots that were sampled both during and after the borer outbreak increased from 19 ± 3 to 34 ± 4 per cent of standing red oaks, resulting in significantly reduced red oak basal area and stem density in these stands. Mean size of red oaks did not change significantly during this time period, implying that all size classes experienced mortality. After red oak borer populations subsided, oak-hickory survey plots experienced increases in red oak mortality levels during a drought year (2006) and after an ice storm (2009), which suggests that these stress events, in addition to prior red oak borer infestation, could have had some influence on tree mortality.

Introduction

Forests dominated by oaks (*Quercus spp.*) are common in the Northern Hemisphere. Equally common is the concept that those forests experience dieback (i.e. leaf loss that begins at the tips of branches in the canopy that can also recover through re-growth) and mortality events (i.e. widespread die-off of a particular genus or species of an advanced age class) through a poorly understood aetiology of insect attack (e.g. Wood *et al.*, 2009), pathogen infection (e.g. Donaubauer, 1998), climate extremes (e.g. Andersson *et al.*, 2011) and senescence (e.g. Mueller-Dombois, 1987) generally labelled as 'oak decline' (Manion, 1991). Evidence suggests oak decline has been an issue for over three centuries in Europe, and arguably recently has expanded in scale and scope (Tomiczek, 1993; Thomas *et al.*, 2002). Causal factors and symptoms reported in Europe differed geographically, yet in all cases aetiology was described as a combination of several biotic and abiotic factors rather than a singular agent (reviewed by Thomas *et al.*, 2002).

In the past 50 years, oak decline events have been reported in upland oak forests in the eastern United States with increasing frequency (McCracken *et al.*, 1990; Tainter *et al.*, 1990; Oak *et al.*, 1991, 2004; Starkey *et al.*, 2004). This may be a result of increased reporting or even-aged stand maturation in fire-suppressed forests following early 20th-century logging of the virgin forests (Millers *et al.*, 1989; Abrams, 1996; Strausberg and Hough, 1997). Prior to European settlement, oaks likely regenerated in uneven-aged conditions (Abrams, 1996), which, in the presence of periodic fire, produced a complex canopy structure that allowed adequate light penetration through the canopy for oak seedling establishment (Johnson, 2004). Oak recruitment in eastern hardwood forests throughout the

20th century has been largely replaced by late succession, shade-tolerant species (Brose *et al.*, 2001; Heitzman, 2003; Soucy *et al.*, 2005).

Episodes of oak mortality are apparently brought on by a complex of stress factors, e.g. poor site conditions, drought, late spring frost, defoliator and/or wood borer outbreaks and root rot (Manion, 1991), and tend to occur repeatedly in the same locations (Millers *et al.*, 1989). An oak decline event has been reported within the state of Arkansas every decade since the 1960s (Millers *et al.*, 1989). Forty-two per cent of Arkansas' timberland is dominated by oak-hickory forests, covering ~3.06 million ha (7.56 million ac) (Rosson and Rose, 2010). A preliminary assessment of the recent oak mortality event that affected Ozark–Ouachita forests estimated that 13 per cent of all trees >12.7 cm in diameter were dead or dying (Guldin *et al.*, 2006), although in stands dominated by red oak species (subgenus *Erythrobalanus*) estimates of mortality ranged from 30 to 100 per cent of basal area (Starkey *et al.*, 2004; Guldin *et al.*, 2006). Several studies indicated that red oaks were more severely affected than white oaks (subgenus *Leucobalanus*) (Guldin *et al.*, 2006; Heitzman *et al.*, 2007; Fan *et al.*, 2008). Red oaks, mainly northern red oak (*Q. rubra* L.), black oak (*Q. velutina* Lam.) and blackjack oak (*Q. marilandica* Muenchh.), comprise one-fourth of the timber volume within interior highland forests of Arkansas, Missouri and Oklahoma, and mortality of one-third of that volume would result in economic losses exceeding US $1.1 billion (Guldin *et al.*, 2006).

Coincident with this oak decline event was an unexpected outbreak of a native wood boring beetle, the red oak borer (*Enaphalodes rufulus* (Haldeman) (Coleoptera: Cerambycidae)), the first record of this insect in association with oak decline (Stephen *et al.*, 2001). Red oak borer has an unusual 2-year life cycle, wherein adults emerge synchronously in odd-numbered years only (Hay, 1969). Within the Ozark and Ouachita National Forests in western Arkansas, red oak borer-related oak mortality was first detected in 1999 (Stephen *et al.*, 2001; Starkey *et al.*, 2004) although borer populations had been building for over 10 generations before the outbreak peaked in 2001 and 2003 (Haavik and Stephen, 2010a). Populations crashed within the following generation (in 2005) (Riggins *et al.*, 2009).

While the outbreak was in progress, several studies assessed red oak borer related oak mortality and its impact on forest structure and composition (Fierke *et al.*, 2007; Heitzman *et al.*, 2007; Fan *et al.*, 2008). Red oak mortality levels since the outbreak have not been quantified. During a previous oak decline event in the Missouri Ozarks, Jenkins and Pallardy (1995) found dying oaks declined for several years prior to eventual mortality. We expect that red oak mortality levels remained high throughout Arkansas forests after red oak borer densities subsided. Investigations of the impacts on the red oak component of Arkansas forests may guide future management decisions following oak mortality events and further understanding of the effects of these events on oak forest succession processes.

The overall goal of this study was to identify changes in red oak mortality in relation to changes in red oak borer population levels across Arkansas forests and to assess changes in the red oak component of these stands with respect to the recent oak mortality event (ca. 1999–2005). Our first dataset was drawn from the USDA Forest Service Forest Inventory and Analysis (FIA) database (USDA Forest Service, 2001; Bechtold and Patterson, 2005). We used forest measurements from recent inventories (1995–2009) collected from a large number of stands throughout the state to assess changes in stem density, basal area and mortality levels. Our second dataset was a more intensive sample derived from examination of red oak borer larval gallery scars preserved within tree rings. This dataset encompassed eight ridge top sites, located within the Ozark and Ouachita National Forests in western Arkansas, and although it was not as extensive as the FIA dataset, we used it to estimate red oak borer population densities in these forests from 1995 through 2009. We sampled ridge tops because they were found to have a higher incidence of red oak borer infestation than other aspects (Fierke *et al.*, 2007). Our specific objectives were to examine the following, from 1995 to 2009: (1) overall patterns of tree mortality among the dominant forest cover types in Arkansas (oak-hickory, oak-pine and loblolly-shortleaf pine) to assess baseline tree mortality levels and compare them to red oak mortality levels; (2) average trends in red oak mortality with respect to trends in red oak borer population densities; (3) basal area and stem density of live trees and live red oaks in average oak-hickory stands (i.e. FIA plots); and (4) red oak seedling/sapling regeneration.

We hypothesized that the slow physiological decline of red oaks would result in increased red oak mortality following the exponential decline of red oak borer populations. In average oak-hickory stands, we expected that live red oak basal area would decrease as a result of this mortality, and live tree basal area would also decrease with the loss of many of the dominant and co-dominant red oaks from these stands. We predicted that live tree densities would remain the same or would increase as understorey species recruitment increased in canopy gaps provided by dying red oaks and that red oak stem density would decrease due to mortality of dominant trees and limited presence of oak regeneration.

Methods

Red oak borer study sites and climate

We located accessible ridge top areas of oak-hickory forest type with a Geographic Information System (Environmental Systems Research Institute's ArcGIS 9.2 software; ESRI, 2006). For this step, we downloaded data layers from GeoStor (run by the Arkansas Geographic Information Office), the University of Arkansas Center for Advanced Spatial Technology and the USDA Forest Service Geospatial Data page. We then confirmed that sites were infested with red oak borer by ground observations of red oak mortality and borer exit holes on the lower portion of red oak boles (Fierke *et al.*, 2005).

Because red oaks, specifically northern red oak and black oak, are preferred by red oak borer over white oaks (Hay, 1974; Galford, 1983), ground-level searches for study sites were biased towards locations where red oaks were dominant. This was done to increase the likelihood that individual trees selected had been attacked and thus would provide a record of borer population levels during the recent outbreak. Previous research indicated that borers were most common where host species were dominant and on dry south-facing slopes or ridge tops (Fierke *et al.*, 2007). We selected eight sites: four were located within the Ozark National Forest and four were located within the Ouachita National Forest (Table 1). In the summer of 2008, we sampled 7 to 10 variable radius points per site using a prism with basal area factor of 1 m^2 ha^{-1} to determine live tree and live red oak basal area at each site. Each sampling point was a sufficient distance from the others to avoid overlap in sampling radii. In the summer of 2010, we installed four fixed radius subplots at each of the eight sites according to FIA plot design (see *FIA data* section) to obtain a final estimate of red oak mortality following the red oak borer outbreak as well as to measure live tree and live red oak stem density (Table 1).

Climate in the Ozark/Ouachita region is temperate with hot summers and mild winters. From 1909 to 2009, mean ± standard deviation January temperature was 3 ± 2.5°C, mean August temperature was 26 ± 1.5°C and the annual mean was 15 ± 8.4°C (NCDC, 2009). Most precipitation occurs during spring and fall, totalling ~115 ± 19.8 cm in the Ozark Mountains and 127 ± 21.0 cm in the Ouachita Mountains (NCDC, 2009). Rock formations of limestone, sandstone and shale comprise much of the Ozark Plateau, which is characterized by deep valleys, steep ledges and cliffs with elevations up to 750 m with slopes facing all cardinal directions (Adamski *et al.*, 1995). The Ouachita Mountains are oriented such that ridges run east to west with maximum elevations reaching 790 m, where upper slopes are steep, gradually levelling off at lower elevations into U-shaped valleys (Viele and Thomas, 1989). Dominant soil types are alfisols and ultisols and are generally rocky, acidic and clay rich, with low organic matter content (Adamski *et al.*, 1995; Allgood and Persinger, 1979).

Red oak borer population densities

We removed 10 surviving co-dominant northern red oaks from each site, except Cowell (n = 9; Table 1), for a total of 79 trees sampled. We cut ~5-cm-thick cross-sections with a chainsaw, either in the field or later from 0.5-m-long logs at the laboratory. The number of cross-sections collected per tree varied according to tree height and ranged from 14 to 69 consecutive cross-sections from lower boles. This was based on a previously developed optimal sampling system that required a sample from 20 per cent of tree boles (see Haavik and Stephen, 2011). To smooth the chainsaw cuts, we used a hand-held planer on the top and bottom surface of each cross-section. We then sanded both surfaces with a hand-held electric belt sander using progressively finer sandpaper: 80, 120, and finally 220 grit.

Table 1: Locations and general information regarding ridge top sites sampled intensively for red oak borer populations

Site name	Site coordinates*	Red oak (% of all trees†)	Red oak mortality (% of red oaks)	Stand age (years)	Live tree density (trees ha^{-1})	Live red oak density (trees ha^{-1})	Live tree basal area (m^2 ha^{-1})	Live red oak basal area (m^2 ha^{-1})	Mean of bole sampled
Mule Farm	0413799, 3954569	27	56	78	66	10	17.0	7.2	28.95
Red Star	0453072, 3970882	60	40	74	83	44	19.4	13.3	22.00
Cowell	0488219, 3967434	63	39	69	92	49	20.1	14.1	21.75
Stack Rock	0507522, 3969016	20	44	83	92	12	20.1	8.4	24.80
Ozarks sites (mean ± SE)		43 ± 11	45 ± 4	76 ± 3	83 ± 6	29 ± 10	19.2 ± 0.7	10.8 ± 1.7	24.4 ± 1.67
Dry Creek Mtn	0430992, 3878916	64	14	78	68	44	16.4	10.4	22.00
Flatside	0508656, 3857809	26	50	77	63	12	18.5	9.1	21.75
Fork Mtn	0405150, 3812227	47	60	79	83	24	9.5	5.3	24.80
Talimena	0367171, 3838821	67	67	88	83	5	12.3	3.9	13.65
Ouachitas sites (mean ± SE)		51 ± 9	48 ± 12	81 ± 3	74 ± 5	21 ± 9	14.2 ± 2.0	7.2 ± 1.5	20.55 ± 2.40

Ten trees were intensively sampled at each site except for Cowell (n = 9), basal area measurements were made in 2008 and density and red oak mortality were measured in 2010 at all sites. The first four rows were sites in the Ozark National Forest and the last four rows were sites in the Ouachita National Forest.
* UTM Zone 15N.
† Standing live and dead trees included.

We dated and aged the cross-sections according to date of felling and cross-dated the lowest cross-section from each tree with master chronologies developed individually for each study site according to standard techniques (Douglass, 1941; Stokes and Smiley, 1996). We cross-dated the remaining cross-sections according to the felling date and signature dendrochronological years in the region: dry years in 1972 and 1988 and a wet year 1992. Red oak borer larvae cross the cambial boundary between phloem and sapwood tissue during their second season of feeding which creates a wound response in the host tree that results in a scar which becomes preserved within that current year's growth ring. We then dated scars caused by the red oak borer; we first identified each scar as the remains of a red oak borer larval gallery by its distinctive shape (Haavik and Stephen, 2011) and then gave it a unique identification number, marked on the top surface of cross-sections to ensure that scars were not under- or over-counted.

To examine the red oak borer outbreak and tree mortality patterns in the context of climate conditions from 1995 to 2009, we utilized climate data from the National Oceanic and Atmospheric Administration averaged across Arkansas climate divisions one, two, four and five (NCDC, 2009). These divisions encompass a region which includes both the Ozark and Ouachita National Forests. We found the July Palmer Drought Severity Index (Palmer, 1965) to be the climate variable most highly correlated with northern red oak growth patterns (Haavik *et al.*, 2011).

FIA data

We downloaded the Arkansas FIA database (FIA DataMart, 2010) and utilized forest measurement data from the region. These were permanent sample plots with fixed plot radius that have been repeatedly sampled every 5–7 years in successive inventory cycles. Plots are organized nationally as a hexagonal grid with one plot per 2428 ha (6000 ac) (Bechtold and Patterson, 2005). Each ground plot has four points, the first of which is central, with points two through four located 36.6 m (120 ft) from the first point at azimuths of 0, 120 and 240° (Bechtold and Patterson, 2005). Each point is located at the centre of a 7.3-m (24-ft) fixed radius subplot where all live and dead trees >12.7 cm (5.0 in) in diameter at breast height (d.b.h., 1.37 m from the ground) or greater are measured (Bechtold and Patterson, 2005). Each subplot also contains a 2.1-m (6.8-ft) fixed radius microplot where saplings 2.5- to 12.4-cm d.b.h. (1–4.9 in) and seedlings <2.5 cm (<1 in) are measured (Bechtold and Patterson, 2005). All four subplots total 0.07 ha (1/6 ac) and all four microplots total 0.005 ha (0.01 ac) (Bechtold and Patterson, 2005).

Only 18.8 per cent of Arkansas timberland is in federal ownership, so we queried the Arkansas FIA database to identify all plots on federal forested land sampled from 1995 to 2009 (n = 1257). We removed plots affected by timber harvesting (n = 210) as well as plots of forest types other than oak-hickory, oak-pine or loblolly-shortleaf pine (n = 10). All plots were sampled during the 1995 inventory and only 20 per cent of all plots were sampled 2000–2009. Data recorded during the 1995 inventory also differed from those recorded from 2000 to 2009. Forest types were not assigned within the database for the 1995 inventory, so we assigned forest type to these plots based on dominant species present. We also considered composition of each of the three forest types from other inventory years as a guide for 1995 assignments based on numbers of oaks, pines and other hardwoods within each plot. From the remaining plots (n = 1037), the data fields that we used were dominant forest type, inventory year (1995, 2000 or 2002–2009), stand age, count of live trees, count of live red oaks, count of standing dead trees, count of standing dead red oaks, live tree basal area and d.b.h. of all trees. From these data, we calculated overall tree mortality as a percentage of all standing trees >12.7 cm d.b.h. for all plots. Stand age was not included for the 1995 inventory year, so we computed mean stand age for plots sampled in 2000. Mean stand age in 2000 for loblolly-shortleaf pine forest type was 61 ± 5 (SE) years, mean stand age in 2000 for oak-pine forest type was 50 ± 6 (SE) years and mean stand age in 2000 for oak-hickory forest type was 68 ± 3 (SE) years. Since stand age varied little within forest types, we did not separate mortality estimates by stand age. For oak-hickory plots, we also calculated red oak mortality as a percentage of standing red oaks per inventory year, change in red oak mortality between inventory years, live tree stem density (trees ha^{-1}), live red oak stem density (trees ha^{-1}), live tree basal area (m^2 ha^{-1}) and live red oak basal area (m^2 ha^{-1}).

Data analyses

We conducted all data analyses using SigmaPlot® 11 (Systat Software Inc., 2008). We combined red oak borer densities per generation from all sites to obtain an overall regional Ozark–Ouachita perspective on population levels throughout the outbreak (see Haavik and Stephen, 2010b). We employed repeated-measures analyses of variance to examine changes in forest measurements of oak-hickory plots between two time periods: outbreak and post-outbreak. Sixty-two oak-hickory FIA plots were re-sampled during both of these time periods. Too few oak-hickory FIA plots were re-sampled either before and after or at all three time periods (i.e. before, during and after the outbreak) to enable analysis for all three time periods (n = 9 and 11, respectively). We created separate models for mean live tree stem density, mean live red oak stem density, mean live tree basal area, mean live red oak basal area, mean live tree d.b.h. and mean live red oak d.b.h. as response variables with time period as a fixed effect. Outbreak time periods were determined in a previous study (Haavik and Stephen, 2010a). To assess violations of model assumptions, we examined studentized residual plots, normal probability plots and the Shapiro–Wilk test for normality of residuals (Shapiro and Wilk, 1965). If assumptions were violated, we transformed response variables by square or square root. All figures and tables report means as untransformed values, statistical significance was set at $P < 0.05$ and all error terms represent 1 SE from the mean.

Results

Mortality occurred within FIA plots of all three forest types and fluctuated somewhat among inventory years, although it ranged from 1 to 20 per cent of standing trees in most plots during this time (Figure 1). Percentage of FIA plots that did not experience any tree mortality among all inventory years was 10 per cent of standing trees for oak-hickory, 16 per cent of standing trees for oak-pine and 20 per cent of standing trees for loblolly-shortleaf pine forest types. Percentage of oak-hickory plots that experienced >10 per cent overall mortality was greatest in 2009 (78 per cent), least in 1995 (18 per cent) and ranged from 37 to 70 per cent in the intervening years. Percentage of oak-pine plots that experienced >10 per cent overall mortality was greatest in 2006, 2007 and 2009 (60 per cent), least in 2000 (5 per cent) and ranged from 16 to 55 per cent in the remaining years. Percentage of loblolly-shortleaf pine plots that experienced >10 per cent overall mortality was greatest in 2006 (58 per cent), least in 2008 (15 per cent) and ranged from 18 to 56 per cent in the remaining years. Most oak-hickory plots either experienced no red oak mortality or >30 per cent of standing red oaks were dead, while relatively few plots exhibited mortality levels between these two extremes (Figure 2). Percentage of plots with no red oak mortality was greater in 1995 before the oak decline event while plots with >30 per cent red oak mortality were more numerous in 2009 after the oak decline event. Only 3 per cent of FIA oak-hickory plots sampled in 1995 experienced >30 per cent red oak mortality, while 35 per cent of those sampled 2000–2009 exhibited >30 per cent red oak mortality. Over 50 per cent of FIA oak-hickory plots that were sampled in 2006 and 2009 exhibited >30 per cent red oak mortality, whereas only 20–45 per cent of plots sampled in other years (excluding 1995) exhibited >30 per cent red oak mortality. At the eight sites intensively sampled for

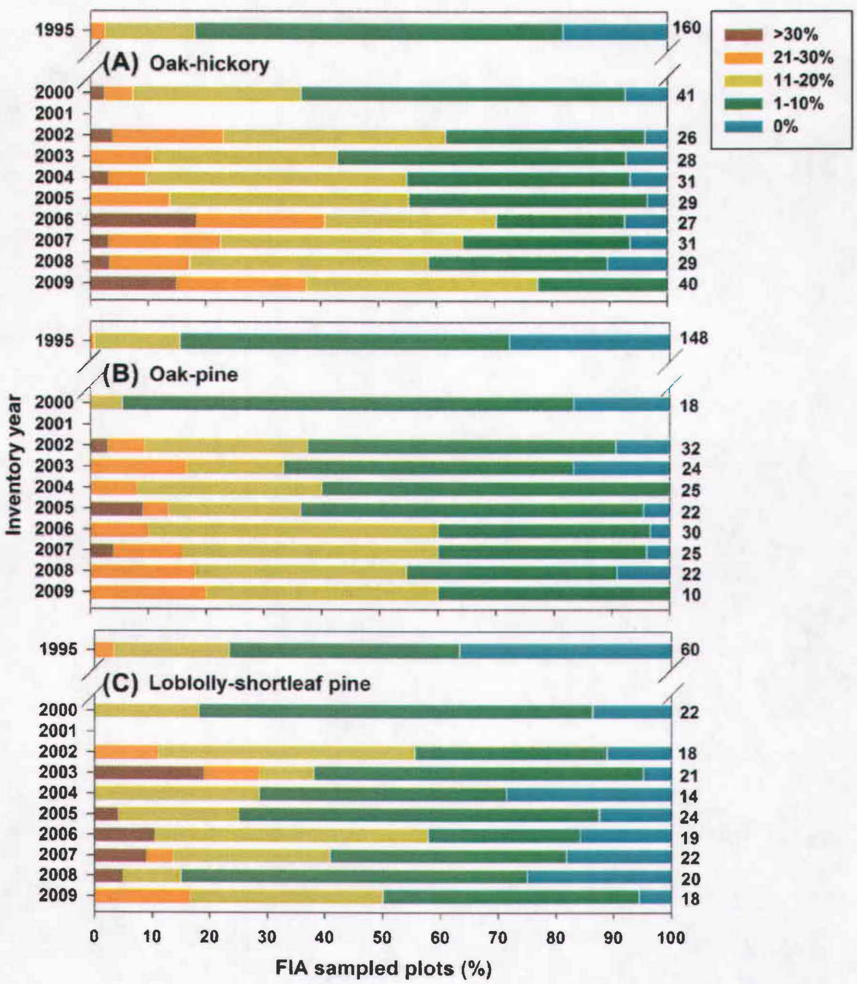

Figure 1. Percentage of FIA sampled plots within each overall mortality class (% of standing trees, key upper right), by inventory year, on federal forested land in Arkansas. Overall tree mortality presented separately for each forest type and excluding plots affected by harvesting. Number of FIA plots sampled each inventory year for each forest type are to the right of horizontal bars of each respective inventory year.

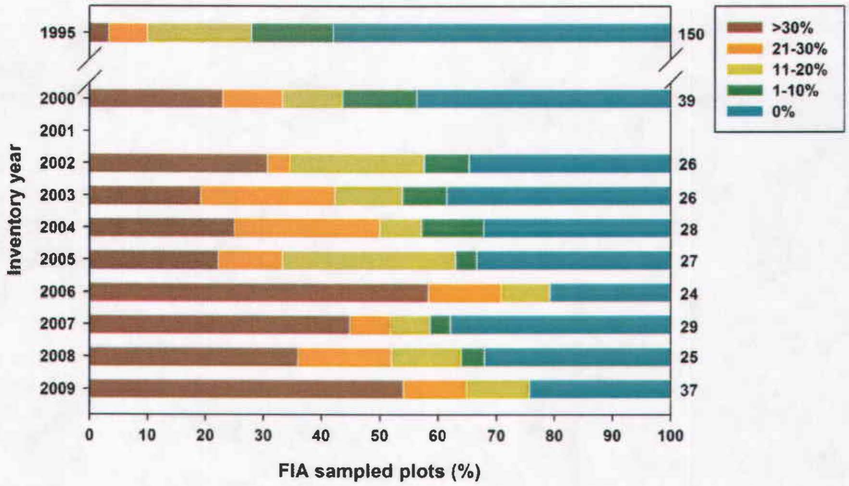

Figure 2. Percentage of oak-hickory forest type FIA sampled plots on federal forested land in Arkansas within each red oak mortality class (% of standing red oaks, key upper right) and by inventory year. Numbers of FIA plots that were not affected by harvesting and contained at least one individual red oak are to the right of horizontal bars of each respective inventory year.

red oak borer populations, cumulative red oak mortality in 2010 ranged from 14 to 67 per cent of standing red oaks, with an overall mean of 46 ± 6 per cent (SE) (Table 1). Red oak mortality at these eight sites in 2010 was within the mortality range of three-quarters of the FIA oak-hickory plots sampled in 2009 (Table 1, >10 per cent in Figure 2).

The mean red oak mortality level in FIA oak-hickory plots increased by 9 per cent between 1995 (pre-outbreak) and 2000 (outbreak, Figure 3A), from 7 to 16 per cent of standing red oaks. Red oak mortality continued to increase between 2000 and 2002 and then annually from 2002 until 2004, but by less in each successive inventory. From 2004 to 2005, red oak mortality in oak-hickory plots remained stable, coincident with exponential decline in red oak borer density (Figure 3A,B). Large increases in red oak mortality occurred between 2005 and 2006 and again between 2008 and 2009, both time periods when the red oak borer outbreak was apparently over. Dry years occurred both during and after the red oak borer outbreak: in 1998 and 2001 and again in 2005 and 2006 (Figure 3C).

Mean red oak mortality in FIA oak-hickory plots sampled both during and again after the outbreak increased by a mean of 15 ± 3 per cent of standing red oaks, where mean red oak mortality was 19 ± 3 per cent of standing red oaks during the outbreak and 34 ± 4 per cent of standing red oaks after the outbreak. For all trees >12.7 cm d.b.h., live tree density also declined significantly (by 33 per cent) between these two time periods in these plots (Table 2). Live red oak density followed the same pattern, where it decreased from 21 per cent of live trees during the outbreak to 17 per cent of live trees post-outbreak (4 per cent decline, Table 2). For all trees >12.7 cm d.b.h., live tree basal area did not change between these two time periods, whereas live red oak basal area declined significantly (Table 2). During the outbreak, red oaks represented 55 per cent of the live tree basal area in FIA oak-hickory plots. Post-outbreak, red oaks only represented 27 per cent of that live tree basal area (28 per cent decline, Table 2). Mean live tree d.b.h. declined significantly between these two time periods, but only by a small amount, while mean live red oak d.b.h. did not change from outbreak to post-outbreak (Table 2). Mean size of red oaks in these re-sampled FIA oak-hickory plots was larger than the overall mean tree size in the same plots. Of the 62 oak-hickory plots sampled both during and after the outbreak, only nine (12.5 per cent) of them contained red oak saplings or seedlings and only two of these contained more than one red oak sapling or seedling at either sampling date. Mean number of red oak seedlings/saplings was 41 ± 25 ha^{-1} during the outbreak and 43 ± 23 ha^{-1} post-outbreak.

Stand age of FIA oak-hickory plots re-sampled during and post-outbreak varied little (mean 71 ± 1 y post-outbreak) and mean stand ages at sites intensively sampled for red oak borer were slightly older (Table 1). These sites had a larger mean red oak component (40–50 per cent of all standing live and dead trees) than FIA oak-hickory re-sampled plots (20 per cent of all standing live and dead trees post-outbreak). Live tree and red oak density was greater at most red oak borer sites post-outbreak than at FIA oak-hickory re-sampled plots (Table 1 *vs* Table 2). Live tree basal area was lower, yet red oak basal area was greater at most red oak borer sites post-outbreak than at FIA oak-hickory re-sampled plots (Table 1 *vs* Table 2). After the outbreak, red oaks represented a mean of 32 ± 8 per cent of live tree density and 53 ± 5 per cent of live tree basal area at red oak borer sites.

Discussion

Mortality levels

Reflective of the recent oak decline event that affected Ozark and Ouachita upland oak-hickory forests, relative

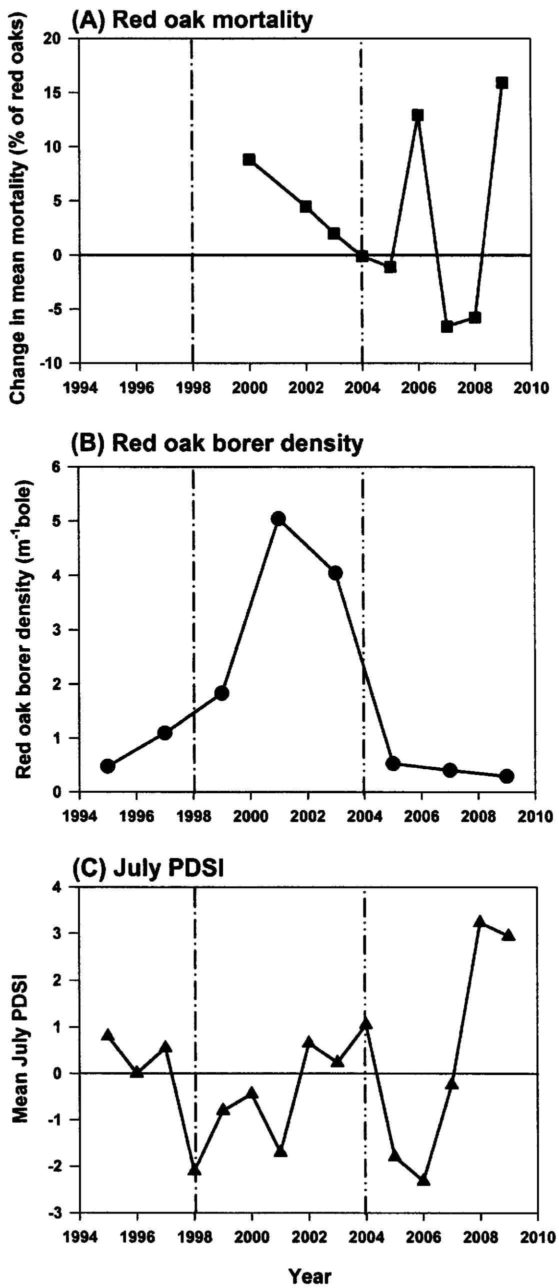

Figure 3. (A) Change in mean red oak mortality as a % of standing red oaks between inventory years in FIA sampled oak-hickory plots on federal forested land in Arkansas (n = 436 for all years, sample sizes by year in Figure 2); (B) red oak borer density per generation representing eight intensively sampled sites within the Ozark and Ouachita National Forests (n = 79 trees) and (C) mean July Palmer Drought Severity Index (PDSI) for regions included in the Ozark and Ouachita National Forests. In (A), red oak mortality increased from 7% to 16% of standing red oaks between the 1995 and 2000 inventories (shown at x = 2000 as a 9% increase). The dash–dot line delineates the transition from pre-outbreak to outbreak time periods and the dash–dot–dot line represents transition from outbreak to post-outbreak time periods.

levels of red oak mortality in FIA sampled oak-hickory plots were greater than overall tree mortality levels among all three forest types during this time period (Figure 1 *vs* Figure 2). Mean red oak mortality levels at FIA oak-hickory re-sampled plots (~20 per cent of standing red oaks during the outbreak) were generally consistent with or lower than those from other studies conducted during the oak decline event and red oak borer outbreak (2000–2003); Heitzman et al. (2007) reported 51–75 per cent of red oak stem density as dead or dying in 2004 and Fierke et al. (2007) found that northern red oak mortality ranged from 11 to 45 per cent of red oak stem density in red oak borer infested stands. Higher estimates of red oak mortality from those studies and intensively sampled red oak borer sites (Table 1) likely resulted from sampling bias towards areas where red oak mortality was more pronounced, whereas the FIA fixed-grid pattern is more representative of average conditions experienced by Arkansas upland oak-hickory forests.

Red oak mortality levels in FIA oak-hickory plots increased at the onset of the outbreak between the 1995 and 2000 inventories (Figure 3), likely in response to the oak decline event and concurrent exponential increase in red oak borer populations. As borer densities declined, annual increases in red oak mortality also declined and levelled off. Red oak mortality spiked again in 2006 and 2009, after red oak borer populations had subsided, which may have been a consequence of region-wide drought from 2005 to 2006 (NCDC, 2009) and a severe ice storm that affected the Ozarks in late January 2009 (Barjenbruch, 2009). Ice storm damage can range from loss of small branches to tree mortality and the level of damage often varies throughout the area impacted by a storm depending on local weather conditions, topography, vegetation and stand density (Bragg *et al.*, 2003). Effects of the 2009 ice storm were variable throughout the Ozark National Forest and data from aerial surveys estimated that 20 per cent of the forest was severely impacted (>50 per cent crown loss and/or bole damage, USDA Forest Service, 2009).

Past surveys of oak in Arkansas revealed that increases in mortality were correlated with drought events (Rosson, 2004). Studies indicate that while drought is related to declining growth rates, oaks can endure several drought events before mortality results (Tainter *et al.*, 1990; Jenkins and Pallardy, 1995), likely due to their many adaptations to dry conditions such as deep roots, xeromorphic leaves and low water potential threshold for stomatal closure (Abrams, 1996). This resiliency may be compromised by simultaneous additional stress factors, such as red oak borer infestation, stand aging/senescence (Mueller-Dombois, 1987), infection by *Armillaria spp* (Bruhn *et al.*, 2000; Kelley *et al.*, 2009), crown degradation from recent ice storms or the additive effects of several drought events occurring over the course of several decades (Haavik *et al.*, 2011). Red oak recovery from the effects of combined stress events has not been well studied in North America; what little is known about it has been measured at the stand level. The combined stress of drought and nutrient deficiency was linked to mortality of northern red oaks in Pennsylvania, and trees on high mortality plots did not recover in basal area

Table 2: Results of repeated-measures analyses of variance of density, basal area and tree size in re-sampled FIA oak-hickory plots on federal forested land in Arkansas

Model	Outbreak, mean ± SE*	Post-outbreak, mean ± SE*	Degrees of freedom	*F*-statistic	*P* value
Live tree density (trees ha^{-1})	96 ± 3a	64 ± 2b	1,61	153.06†	<0.001
Live red oak density (trees ha^{-1})	20 ± 2a	11 ± 1b	1,58	61.05	<0.001
Live tree basal area (m^2 ha^{-1})	22.2 ± 0.7a	22.2 ± 0.7a	1,54	0.02	0.901
Live red oak basal area (m^2 ha^{-1})	11.7 ± 1.2a	6.2 ± 0.6b	1,58	50.54	<0.001
Live tree mean d.b.h. (cm)	23.2 ± 0.5a	22.1 ± 0.4b	1,59	15.50	<0.001
Live red oak mean d.b.h. (cm)	33.3 ± 1.0a	32.9 ± 1.1a	1,52‡	0.26	0.611

Inventory years included outbreak = 2000, 2002 and 2003 and post-outbreak = 2004–2009. Plots that did not contain red oaks were removed from red oak density and red oak basal area models.

* Means followed by different letters represent significant differences.

† Response data square transformed to meet model assumptions.

‡ Two outliers removed from model.

growth following a drought event (Demchick and Sharpe, 2000). During a previous decline event in Pennsylvania, red oak recovery began even as a drought event continued, yet only after insect defoliation ceased (Nichols, 1968).

Red oak borer infestation was often reported as coincident with red oak mortality during the recent outbreak and oak decline event, yet it does not appear to be a singular cause of mortality. Fan et al. (2008) discovered that crown dieback was positively correlated with borer exit holes, but mortality was significantly correlated with dieback, not exit holes. Haavik and Stephen (2010b) found that dead northern red oaks did not necessarily contain higher densities of borers than surviving trees, but they did support greater larval survivorship. Combined effects of red oak borer infestation, drought and other potential environmental stressors on red oaks likely resulted in increased red oak mortality from 1995 to 2002, yet spikes in red oak mortality in 2006 and 2009 could not be attributed to extant red oak borer infestation (Figure 3). It is possible that the stress caused by borer infestation during the outbreak rendered red oaks more susceptible to mortality during the next drought event in 2005 to 2006.

Whether red oak mortality rates stabilize, decline or continue to rise in the upcoming inventory years, the question remains, which individual trees are most likely to die? Our results indicate that mortality occurred among all size classes at the stand level since there was no significant change in d.b.h. during the red oak borer outbreak compared with after it (Table 2). A recent study identified tree characteristics associated with mortality during an endemic (non-oak decline) time period in the Missouri Ozark Highlands. Those individuals were slow growers, suppressed or of intermediate crown class with a lower basal area than their competitors (Shifley *et al.*, 2006). While suppressed individuals died during the recent oak decline event, trees of all size classes were affected (Heitzman, 2003; Guldin *et al.*, 2006). Some survivors of this decline event experienced a growth release as neighbouring trees died, freeing up resources within overcrowded stands (Haavik and Stephen, 2010b). Other survivors' growth rates did not change or continued to decline, implying that they were unable to take advantage of reduced competition. We predict that these individuals will be most likely to die during the next mortality event as evidenced by their slowing growth rates (<13.7 mm $decade^{-1}$, Haavik and Stephen, 2010b) signifying limited resiliency to additional stress events.

Changes in oak-hickory forest structure

Red oak basal area and stem density declined in FIA oak-hickory plots re-sampled both during and after the red oak borer outbreak (Table 2), resulting in reduced numbers and biomass of mature, dominant red oak in Arkansas oak-hickory stands. Live tree density declined between the two time periods, implying self-thinning or mortality of dominant and co-dominant trees while stem recruitment in diameter classes >12.7 cm was low. These forests were likely in the understorey re-initiation stage at this time, a stage beyond which a majority of self-thinning occurs (Johnson *et al.*, 2002; Johnson, 2004). However, there was only a 4 per cent decline in live red oak stem density compared with a 33 per cent decline in live tree density between the two time periods (Table 2), suggestive of mortality of other co-dominant species, such as white oaks. Red oak seedling/sapling densities were extremely variable, non-existent in most FIA plots and similar during and after the outbreak, indicating that red oak regeneration was low and has not changed as of yet following the oak mortality event.

Red oak mortality had no obvious effect on live tree basal area in these stands, which suggests that basal area of other species increased during this time period. Dying dominant red oaks likely produced canopy gaps that freed up resources in formerly crowded stand conditions, allowing neighbouring species in the canopy or understorey to experience increased radial growth. We found evidence of this among northern red oaks in an earlier study that examined radial growth prior to and during the red oak borer outbreak (Haavik and Stephen, 2010b). Mean size of red oaks did not change after the oak mortality event which indicated that mortality was not size dependent and revealed the lack of a red oak component in the understorey, likely a result of current even-aged conditions and past fire suppression in Arkansas oak-hickory forests.

These changes in forest structure (Table 2) were generally consistent with a survey of severely impacted Northern Arkansas oak-hickory stands conducted during one season only (2002), where healthy live red oak basal area was reduced from 11.7 to 2.5 m^2 ha^{-1} (Heitzman, 2003). Healthy red oak density was reduced from 24 to 4.4 trees ha^{-1} (Heitzman, 2003). Stands sampled in that study grouped dead trees together with those that were in advanced stages of decline and may have been biased towards areas experiencing high mortality, such as the sites intensively sampled for this study (Table 1). Healthy trees in that study were probably comparable to live trees in our study, such that 'declining' trees from the 2002 study likely died at some point following the oak decline event and red oak borer outbreak.

Conclusions and management recommendations

Red oak mortality in Arkansas oak-hickory forests increased in plots sampled during and again after the red oak borer outbreak, which resulted in significantly reduced red oak basal area and stem density in these mature stands. Red oak mortality did not seemingly impact live tree basal area in these stands, which may have been the result of increased growth of neighbouring species in canopy gaps provided by dying dominant red oaks. Red oak mortality level increased by 10 per cent of standing red oaks between the 1995 (pre-outbreak) and 2000 (outbreak) inventory years; thereafter, annual increases in red oak mortality decreased along with declining red oak borer densities. Red oak mortality spiked again after red oak borer populations had subsided during a drought year (2006) and after an ice storm (2009), implying that an additive combination of stress events may have been responsible for mortality. While little oak regeneration was present throughout the past decade, canopy gaps as a result of oak decline or ice damage can affect forest regeneration and future species composition, where species with sprouting potential, such as oaks (Johnson, 2004) may become more competitive than others.

Since drought and low tree vigour appear to contribute to mortality, we suggest that stands at high hazard for red oak borer outbreak be managed using intermediate silvicultural treatments that reduce basal area to promote general tree vigour, with special attention to the red oak component. Thinning, for example, to keep stand basal area between 15 and 20 m^2 ha^{-1} (65–87 ft^2 ac^{-1}) will prevent overcrowding and intense competition for limited resources, especially on ridge top sites. Promotion of species mixes that include both red and white oaks can also mitigate the impacts of species-specific mortality events. Consideration should be given to removal of red oaks in the intermediate or suppressed canopy classes, which are at higher risk of mortality from exogenous disturbance events than the more vigorous dominant or co-dominant red oaks. Restoring fire through prescribed burning in high-hazard stands will also reduce stem density in the mid-storey and understorey, especially by controlling tolerant species competing with oak advance growth. In addition to long-term management strategies, salvage and sanitation cutting applied after the onset of oak decline may even be helpful for mitigating the effects of decline on the remaining red oaks (Dwyer et al., 2007).

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Conflict of interest statement

None declared.

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